FLK West (Lower Bed II, Olduvai Gorge, Tanzania): a new early Acheulean site with evidence for human exploitation of fauna

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Abstract:

This paper presents a detailed taphonomic study of the faunal assemblage from FLK West (Olduvai Gorge, Tanzania), a site with an Acheulean component that dates to 1.7 Ma. The faunal sample analysed here is distributed in different archaeological levels and is associated with a significant lithic accumulation including several large format tools and handaxes. The fauna indicates the proliferation of open environments similar to those found in other Bed II and late Bed I sites. Evidence of anthropogenic activity (e.g. defleshing activities and marrow consumption) has been identified in the form of cut and percussion marks. A photogrammetric and morphometric analysis suggests that these marks were produced with quartzite flakes and not with handaxes. Evidence of interaction with carnivores was also noted; tooth marks were observed on some bones. Such interaction indicates the existence of competition between humans and carnivores for the same ecological niche, and might lead us to reflect on the survival strategies of Lower Pleistocene hominins.

Keywords: taphonomy | Olduvai Gorge | Acheulean | archaeology

Article:

The Acheulean technocomplex is characterized by the production of handaxes, cleavers, picks, large flake blanks, cobbles and tabular clasts (Ambrose 2001; Lycett & Gowlett 2008). The emergence of the Acheulean signals a significant technological change that is currently dated to around 1.7 Ma ago for Kokiselei in Kenya, Konso in Ethiopia and FLK West in Tanzania (Lepre *et al*. 2011; Beyene *et al*. 2013; Diez-Martín *et al*. 2015). Between 1.6–1.4 Ma the

Acheulean spread throughout the African continent (Roche *et al*. 2003) and eventually into Eurasia by the end of the Lower Pleistocene (Goren Inbar *et al*. 2002).

The earliest Acheulean is contemporaneous with so-called 'Developed Oldowan' sites at Olduvai, Koobi fora and Peninj (Leakey 1971; Domínguez-Rodrigo *et al*. 2002). The spatio-temporal overlap of these technocomplexes raises several interesting questions, perhaps the most persistent of which concerns functionality. Several authors suggest that Acheulean sites older than 1 Ma may be associated with the processing of wood or plant resources (Keeley 1980; Schick & Toth 1993; Domínguez-Rodrigo *et al*. 2001). This would explain why some Acheulean sites with large accumulations of handaxes (e.g. Olorgesaillie or Peninj) lack butchered faunal remains (Isaac & Isaac 1977; Domínguez -Rodrigo *et al*. 2002) and why other sites, such as TK Lower Floor (Olduvai Gorge), show no direct relation between the fauna and the stone tools found in the same levels (Leakey 1971; Yravedra *et al*. 2016). The poor preservation of bone surfaces at TK did not allow the identification of the agent involved in the bone accumulation. Nevertheless, several green fractures and a single percussion mark have been identified (Yravedra *et al*. 2016). At contemporaneous 'Developed Oldowan' sites (e.g. BK at Olduvai, the ST Complex at Peninj, some sites at Koobi Fora in Kenya, Swartkrans in South Africa), in contrast, the faunal and lithic remains appear to be functionally associated, as bones bear anthropogenic marks (Bunn 1981; Domínguez-Rodrigo *et al*. 2002; Pickering *et al*. 2004; Domínguez-Rodrigo *et al*. 2007, 2009a, 2014a; Egeland & Domínguez-Rodrigo 2008; Pobiner *et al*. 2009; Organista *et al*. 2015).

The site of Frida Leakey Korongo West (FLKW) at Olduvai has recently provided evidence for the association of early Acheulean tools with carcass exploitation (Diez-Martín *et al*. 2015). In this paper we present a comprehensive taphonomic study of the FLKW fauna from each of the archaeological levels. We also analyse the identified cut marks using a photogrammetric and geometric morphometric approach to determine the type of tool used in the processing of carcasses. Finally, we characterize the palaeoecology of the FLKW fauna in relation to the other Bed II sites.

The site of FLKW

FLKW was discovered in 2013 by The Olduvai Palaeoecology and Paleoanthropology Project (TOPPP). FLKW is located just west of the famous FLK site (Fig. 1) at the base of Bed II (Fig. 2). The chronology of FLKW is situated between 1.698±0.015 and 1.664±0.019 Ma (Fig. 2). These chronological constraints situate FLKW right above Tuff IIA, which was previously dated to *c*. 1.7 Ma. Hay (1976) highlighted that throughout this region, most of Bed II is eroded away by later incision. At locality 45 (FLK) this erosion affected the Lemuta Member and Tuff IIA, creating the first regional discordance identified. The discordance represents a sedimentary change: above the discordance only medium- to high-energy sediments were deposited, in contrast with the underlying waxy clays. FLKW is precisely situated at the base of this transition, before the waxy clays give way to the detritic and erosive sedimentation of the overlying stratigraphical sequence (Diez-Martín *et al*. 2015).

Figure 1. Location of FLKW in northern Tanzania (map modified from Hay 1976).

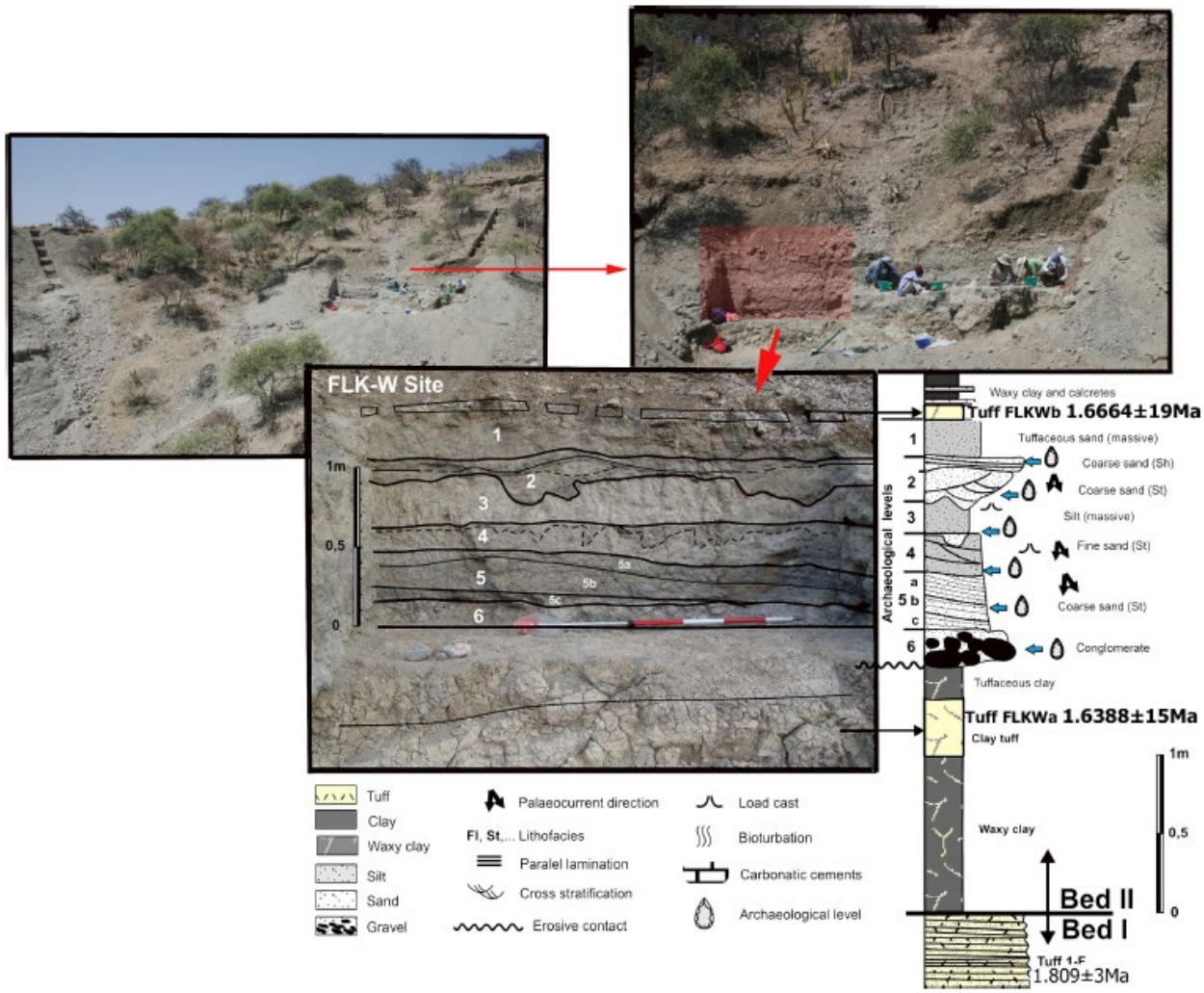

Figure 2. Stratigraphy of FLKW. Photographs and drawing modified from Diez-Martín *et al*. (2015).

FLKW is located in a fluvial palaeochannel where six stratigraphical levels with fauna and lithic remains have been defined (Diez-Martín *et al*. 2015). Level 6 is a 20-cm-thick matrix-supported

conglomerate composed of blocks, cobbles and gravels (2–150 mm) within a matrix of coarse sand. Level 5 is composed of coarse sand. Level 4 is composed of medium-grained sand and well-sorted fine tuffaceous sands. Level 3 is a massive clayish silt without flow structures. Level 2 is an erosive and complex unit, and Level 1 is formed by massive fine-grained homogeneous sand and silt.

A total of 2120 lithic artefacts has been discovered at FLKW. These tools were produced with local raw materials: quartzite, volcanic rocks and chert (Diez-Martín *et al*. 2015). Handaxes and large flakes dominate the assemblage, especially in Levels 5 and 6 (Diez-Martín *et al*. 2015). A preliminary taphonomic study provides direct evidence for the functional association of the lithic artefacts and the faunal remains (Diez-Martín *et al*. 2015), making FLKW one of the few Lower Pleistocene sites with Acheulean tools that can be clearly linked to the consumption of carcasses. Here, we built on that preliminary foundation with a detailed taphonomic and palaeoecological analysis of FLKW.

Sample

A total of 1042 remains from FLKW Levels 1–6 was analysed for this study. To analyse the cut marks and determine the kind of stone tool used we compared the morphology and section of the cut marks with experimental marks. The experimental reference sample includes 107 cut marks produced with quartzite flakes from the Naibor Soit, 85 cut marks made with basalt flakes collected at Olduvai Gorge (Maté-González *et al*. 2016) and 122 cut marks produced with handaxes of Naibor Soit quartzite. Quartzite and basalt are the two main raw materials found in the Bed II sites (Hay 1976; Kyara 1999). Basalt outcrops can be found in the river channels that flow from the slopes of the Olmoti and Lemagrut volcanoes, 9 km to the east (Kyara 1999). The quartzite found at Olduvai probably derives from Naibor Soit (Hay 1976).

Palaeoecological comparisons were made with assemblages recovered from other sites in Bed II such as HWK3-5, MNK and FCW (Leakey 1971), TK (Yravedra *et al*. 2016), SHK (Domínguez-Rodrigo *et al*. 2014b) and BK (for BK1, BK2 and BK3, see Domínguez-Rodrigo *et al*. (2009b), for BK4 see Domínguez-Rodrigo *et al*. (2014a) and for BK4b see Organista *et al*. (2015)).

Material and methods

Faunal analysis

Taxonomic identifications were based mainly on teeth and reference material. However, in those cases when such determination was not possible, fragments were attributed to animal weight/size classes following Bunn (1982), where ‘small-sized’ is considered sizes 1 and 2, ‘medium-sized’ refers to size 3, and ‘large’ refers to sizes 4–6.

Faunal remains were quantified by number of identifiable specimens (NISP), minimum number of individuals (MNI) and minimum number of elements (MNE). MNE estimates include limb shafts, age, size and biometrics. Elements were quantified according to Yravedra & Domínguez-Rodrigo (2009). For limb bone identifications, factors such as shaft thickness, section shape and

medullar surface properties were considered (Barba & Domínguez-Rodrigo 2005). MNI estimates considered element side and ontogenetic age (Brain 1969).

To assess mortality patterns, specimens were assigned to one of three categories based on tooth eruption and crown wear: infantile, juvenile–prime adult and adult.

Skeletal part profiles were organized into four anatomical regions: cranial (i.e. horn, cranium, mandible and teeth), axial (vertebrae, ribs, pelvis and scapula, *sensu* Yravedra & Domínguez-Rodrigo 2009), upper appendicular elements (humerus, radius, ulna, femur, patella and tibia) and lower appendicular elements (metapodial, carpals, tarsals, phalanges and sesamoids). Long limb bones were further divided into upper (humerus and femur), intermediate (radius and tibia) and lower (metapodial) bones (Domínguez-Rodrigo 1997).

Several procedures were followed to reconstruct site formation processes, assess site integrity and evaluate the contribution of various biogenic agents to the faunal assemblage. Bone fragmentation was analysed according to two variables. First, bones were divided into several categories according to their length: <3, 3.1–5.0, 5.1–10 and >10 cm. Second, shaft preservation was classified following Bunn's (1982) circumference types, where type 1 refers to specimens with <50% of the shaft circumference intact, type 2 to specimens with >50% of the shaft circumference intact and type 3 to specimens with an intact shaft circumference.

The impact of water activity was estimated with fragment size distributions and the presence of abrasion, polishing, rounded bones, and carbonates. Signs of polishing, rounding or abrasion would be expected in transported assemblages, but also in non-transported assemblages exposed to circulating water and mobile sediments, such as those encased in sand strata (Thompson *et al*. 2011). Determining whether or not the assemblage is in primary vs. secondary position is particularly important given the fluvial depositional context of the site.

Weathering was analysed following Behrensmeyer (1978). A high degree of weathering can affect the fragmentation and deterioration of bones. It is important to differentiate whether weathering alterations are affecting bones showing green and/or dry (including diagenetic) breakage patterns. To identify both types of breakage we followed Villa & Mahieu's (1991) criteria. Dry breaks result in abundant breaks that are longitudinal and/or transverse to the axis of the bone and breakage planes that are uneven, rough and possess micro-step fractures. Dry breaks are also characterized by cortical medullary surface angles that are close to 90°. In contrast, green-broken specimens frequently have smoother surfaces and more abundant oblique breakage planes.

Additionally, a systematic search for bone surface modifications was carried out with 10–20× hand lenses (Blumenschine 1995). Diagnostic criteria defined by Domínguez-Rodrigo *et al*. (2009b) guided the identification of cut marks, whereas tooth and percussion marks were recorded following Blumenschine (1988, 1995). For comparative purposes, surface modifications include the evaluation of epiphysis and shaft areas (Blumenschine 1988, 1995). Modifications are also quantified by element type and bone section (Domínguez-Rodrigo 1997; Barba & Domínguez-Rodrigo 2005) based on NISP values. The presence of tooth, percussion

and cut marks is recorded for the entirety of the remains, although estimated percentages include only well-preserved bone surfaces.

Human and carnivore activity can also be identified through breakage patterns. Notches, for instance, which are semi-circular outlines along the otherwise rectilinear edge of a fracture surface associated with a negative flake scar on the medullary surface (Capaldo & Blumenschine 1994; Domínguez-Rodrigo *et al*. 2007), can be produced by both humans and carnivores. Notches can be classified in four groups: A (single notch), B (incomplete notch), C (double-overlapping notch) and D (double-opposing), with humans and carnivores producing different frequencies of each type. Although the dimensions of notches can be measured, these data typically do not reliably distinguish between the two actors, so they are not reported here. By contrast, the angle of fracture resulting from the action of these agents (dynamic loading in the case of humans and static loading in the case of carnivores) has been demonstrated to be more reliable. The platform angles of bone flakes removed during percussion tend to be more acute/obtuse than those of flakes removed during carnivore bone breakage. Using a goniometer, the platform angle was measured at the loading point on the negative scar of the detached flake.

Geometric morphometric and micro-photogrammetric analysis of cut marks

Cut marks were analysed according to micro-photogrammetric and geometric morphometric analyses. The cut marks were selected on the basis of their preservation and general condition. We excluded those marks that display poor cortical preservation owing to weathering, biochemical alteration or the overlap of tooth marks.

High-resolution images obtained through micro-photogrammetry and computer vision techniques were used for the 3D modelling of cut mark sections. Following the methodology of Maté-González *et al*. (2015), oblique photographs and micro-photogrammetrics were used to generate precise metrical models of cut marks. A Canon EOS 700D reflex camera with a 60 mm macro-lenses was used. Specimens were individually placed on a photographic table with lighting adjusted in such a way as to keep the bone continuously well illuminated. The photographic sensor had to be configured at the beginning of the process to adjust focus and brightness. A tripod was used to stabilize the camera during the photographic process. Both the exposure time of the camera and the lighting remained constant during image data capture. The methodology required placing a millimetric scale next to the cut mark to provide a precise measurement reference (see Maté-González *et al*. 2015).

Once the photographs had been taken, they were processed to generate a 3D model for each mark. Photographs were treated with photogrammetric reconstruction software packages in *GRAPHOS* (inteGRAted PHOtogrammetric Suite), Agisoft PhotoScan, PIX4D, and PW (González-Aguilera *et al*. 2013, 2016a, b; Maté-González *et al*. 2015). After producing scaled 3D models, *Global Mapper* software was used to define and measure mark profiles as explained in Maté-González *et al*. (2015, 2016). For data collection between nine and 13 photographs were taken for each mark. The number of photographs varied depending on the geometry of the bone and the shape of the mark. The 3D reconstruction of each mark takes 30–40 min depending on the final number of photos acquired.

Our goal with the reconstructions is to maximize both accuracy and completeness. If the separation amongst images (baseline) increases, the accuracy will improve as the intersection of the perspective rays is geometrically more favourable, but the completeness of the object decreases owing to the similarity of adjacent images. By contrast, if the separation amongst images (baseline) decreases, a better completeness of the object will be obtained, but the accuracy will be poorer because of a worse intersection of the perspective rays.

To contextualize the accuracy analysis of photogrammetric and geo-informatic (PG) methods vs. microscopy given that geometric data are dependent from two different sources (scaling and photogrammetric reconstruction-PHO), the precision of the PG was estimated as follows:

$$\sigma_{PG} = \pm\sqrt{\left(\sigma_{scaling} \cdot GSD\right)^2 + \left(e_{PHO} \cdot GSD\right)^2} \quad (1)$$

where $\sigma_{scaling}$ is the scaling precision established as 1/3 of the pixel (Luhmann *et al*. 2013), e_{PHO} is the reprojection error of the photogrammetric bundle block adjustment expressed in pixels, and GSD is the ground sample distance expressed in m/pixel. In this way, it is possible to obtain a comprehensive and complete comparison at geometric and statistical levels.

Cut marks were measured at mid-length (about 50% of the mark length) as suggested in Maté-González *et al*. (2015). According to such description, the confidence range to measure the marks hardly varies if they were between 30% and 70% of the mark length. A series of measurements including WIS, WIM, WIB, OA, D, LDC, RDC (*sensu* Bello *et al*. 2013) were taken on the mark section and used as quantitative variables (Fig. 3).

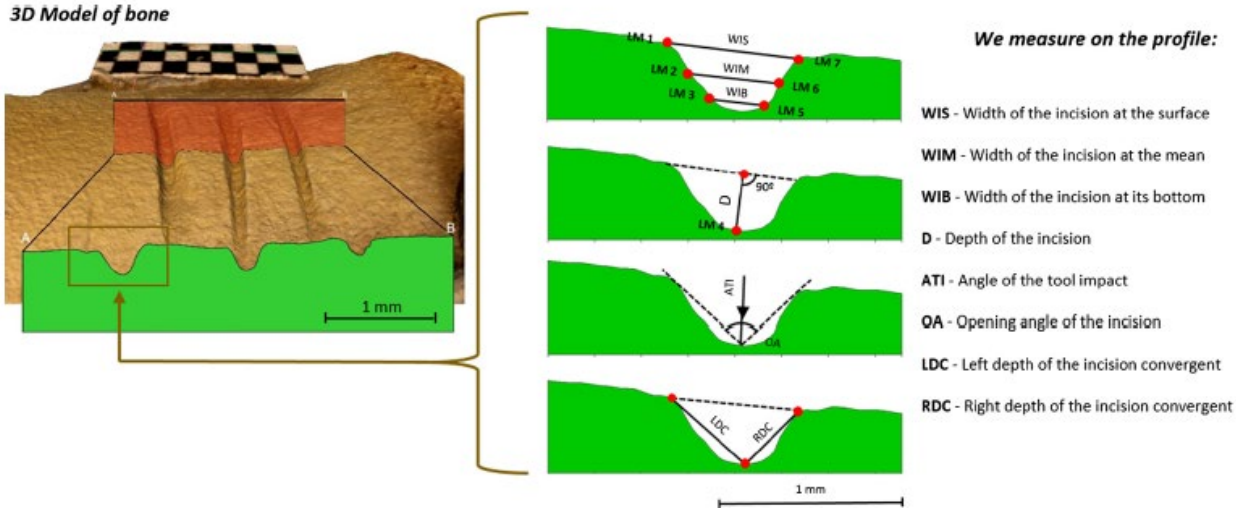

Figure 3. Cut mark measurements and landmarks used in the geometric morphometric analysis.

The measurements for each mark section were later compared with experimental samples of cut marks produced with flakes and handaxes (Fig. S1) made from quartzite and basalt obtained within the Olduvai Basin (Maté-González *et al*. 2016). In this case, seven identical landmarks per section – as shown in Fig. 6 (LM 1–7) – were considered for each mark. Landmarks were digitalized using tpsUtil (v. 1.60) and tpsDig2 (v. 2.1.7), as explained in Maté-González *et al*.

(2015). The locations of the landmarks correspond to the measures considered for the statistical analysis (Fig. 3). LandMark 1 (LM1) was found at the beginning of the left line in the mark section; LM2 appeared in the middle of this line; LM3 was placed at approximately 10% of the right end of the mark (Fig. 3); LM4 was at the very end; LM5, LM6 and LM7 were placed opposite LM3, LM2 and LM1, respectively. The resulting tps file was imported into R (R freeware, www.r-project.org) and analysed using the 'geomorph' library (Sherratt 2014). We conducted a geometric morphometric bidimensional analysis of the seven landmarks (see Fig. LM1–7 of Fig. 6), which were first subjected to a generalized Procrustes analysis (GPA). This technique normalizes the form information by the application of superimposition procedures. This involves the translation, rotation and scaling of shapes defined by landmark configurations. We have incorporates a multivariate principal components analysis (PCA). The PCA estimates similarities and differences of marks on a bidimensional Euclidean space. Plotting of the PCA with confidence ellipses was carried out with the ggplot2 R library. Lastly, a discriminant linear analysis (DLA) was performed to estimate the differences amongst the several groups of marks defined by raw materials. The DLA function is included in the MASS R package.

Palaeoecological analyses

For the palaeoecological analysis we compared the taxonomic profiles of FLKW with those identified at other Bed II sites. Animal species were grouped according to their palaeoecological characteristics, and were plotted in three separate groups: (i) those corresponding to wooded ecosystems, (ii) those corresponding to water sources and (iii) those corresponding to open savanna biomes.

Animal species were distinguished and tabulated (using MNI) by tribe. This analysis allows the discrimination of species and of the types of environments that are represented. A ternary plot was used to group the data from FLKW and other Bed II sites and then link these data to the major bovid tribes of Africa. The ternary graph was programmed in R (library ggtern) using all the data from each bovid group. The bovid groups considered were Alcelaphini and Antilopini, Reduncini and Bovini, and Tragelaphini and Aepycerotini.

Results

Taxonomical, mortality and skeletal profiles

The FLKW fauna includes a large array of species (Table 1), although it is dominated by open-habitat taxa. Alcelaphines, antilopines and equids are the most common taxa throughout the stratigraphical sequence. Other animals associated with the presence of water such as *Hippopotamus*, or species adapted to mixed environments such as *Kobus* and *Tragelaphus*, do also appear in some levels.

Table 1. Taxonomic profiles at FLKW by NISP and MNI

Species	**Level 1**		**Level 2**		**Level 3**		**Level 4**		**Level 5**		**Level 6**	
	NISP	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**
Bird	1	1										
Tortuca									1	1		
Crocodile	1	1										
Connochaetes sp.									4	2		
Megalotragus sp.			2	1			1	1	1	1	3	1
Alcelaphini 3a	2	2			1	1	1	1	5	2	6	1
Alcelaphini 3b									1	1		
Alcelaphini 2	1	1					5	2	3	1		
Hippotragus gigas									1	1		
Tragelaphini sp.									1	1		
Kobus sp.							1	1				
Antidorcas							1	1				
Gazella sp. size 1							4	1				
Gazella sp. size 2	1	1					4	1	1	1		
Syncerus sp.	1	1									1	1
Pelorovis oldowayensis									1	1		
Giraffidae									1	1	1	1
Kolpochoerus sp. size 2									3	1	1	1
Kolpochoerus sp. size 3	1	1					1	1	2	1	3	1

Species	Level 1		Level 2		Level 3		Level 4		Level 5		Level 6	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Metridiochoerus sp.									2	1	6	2
Suidae size 3			1				2	1	1	1	1	1
Elephas sp.	2	1	2	1	2	1	1	1				
Equus oldowayensis	2	1							9	2	8	1
Hipparion cornelianum	1	1									9	3
Rhinocerontidae									1	1		
Hippopotamus sp.	7	2	1	1			10	1				
Crocuta crocuta									1	1		
Indet. size 1							5		4		5	
Indet. size 2	2				3		20		45		24	
Indet. size 3	8		4		6		22		53		35	
Indet. size 3a	3				6		11		39		30	
Indet. size 3b	2				1		7		22		46	
Indet. size 4	12		2		1		17		40		36	
Indet. size 5	12		1		2		11		7		12	
Indet. size 6					1		2		3		2	
Indet.	17		18		14		84		105		103	
Total	76		31		37		210		357		332	

Levels 1, 2 and 3 are the least representative of the sequence. Only 75 remains were found in Level 1, 31 in Level 2 and 37 in Level 3, representing at a minimum 12, three and two individuals, respectively (Table 1). These MNIs are probably underestimates because indeterminate remains assigned to size 2–6 animals were not considered. Alcelaphini is the most commonly represented tribe, appearing in all three levels. Elephant remains were also observed in all levels, but are not as abundant. Suidae and buffalo are only represented in Level 1, as well as gazelles and equids (both *Equus* and *Hipparion*). Finally, *Hippopotamus* appears in Levels 1 and 2. Level 1 shows the widest taxonomic range, with a total of eight mammal species represented in addition to two bird and two reptile species. In Level 1 species adapted to open areas co-occur with species associated with watercourses (e.g. hippopotamus, crocodile and buffalo).

Levels 4–6 preserve much higher frequencies of remains, with more than 200 specimens representing more than 10 individuals in each level. Level 4 has a wide faunal range with eight species, most of them adapted to open areas. This level also includes species such as waterbuck and hippopotamus that require the presence of water in the vicinity. Level 5 also shows wide faunal diversity, with a total of 12 identified species. Amongst the Level 5 species, there is a clear predominance of animals adapted to open environments (Alcelaphini, Antilopini, Suidae*, Rhinoceros,* Giraffidae). Species best suited to bushy habitats such as Tragelaphini and *Pelorovis* are also present. Level 6 has a less diverse fauna and open-habitat species are clearly predominant.

Age patterns suggest a predominance of adult individuals. No infants were identified and only two juveniles were found in Level 1 – one *Hippopotamus* and one Alcelaphini size 3a.

As mentioned above, the upper levels are not very representative as they contain few elements (Table 2). Only in Level 1, there are more than 20 elements belonging to large animals; most of these are cranial elements, although axial and appendicular bones are also present. Levels 2 and 3 have very few elements and those are mainly cranial elements. In Level 3 only middle-sized animals are present, accounting for >10 elements, including teeth and long bone shafts (Table 2). Owing to the small sample sizes no significant conclusions could be drawn, although the absence of epiphyses and the low axial MNE are notable.

Levels 4–6 show a more even skeletal representation; almost all taxonomic groups are represented by more than 20 elements. Nevertheless, in proportion to the MNI, a large osteological bias is apparent. In Level 4, for example, there are bones of all taxonomic groups, but within each group there are certain anatomical elements missing. Amongst small-sized animals cranial elements are abundant, especially teeth, whereas appendicular and axial elements are scarce. Medium-sized animals are better represented by appendicular elements than by axial and cranial bones. Amongst large-sized species there are more axial elements than appendicular elements (Table 2).

Table 2. Skeletal profiles (MNE) of Levels 1, 2, 3, 4, 5 and 6. where small includes sizes 1 and 2; middle, sizes 3, 3a, 3b; and large, sizes 4, 5, 6

	Level 1 MNE			**Level 2 MNE**			**Level 3 MNE**			**Level 4 MNE**			**Level 5 MNE**			**Level 6 MNE**		
	Small	**Middle**	**Large**	**Small**	**Middle**	**Large**	**Small**	**Middle**	**Large**	**Small**	**Middle**	**Large**	**Small**	**Middle**	**Large**	**Small**	**Middle**	**Large**
Horn								1		2				1	1		2	
Skull			1					1					2	4	2	1	2	1
Maxilla													1	1		1	1	
Mandible			2			1				2		2		2	1	1	2	1
Teeth	3	4	13		5	4		2	1	10	8	5	4	25	4	0	29	3
Vertebrae		1	2				1		2	3	2	8	4	5	6	2	3	3
Rib		1	4			1		1		2	2	2	1	4	4	1	6	2
Scapula											1	0	2	3	1		2	
Humerus																		
Proximal end												1		1		1		
Shaft	1	1	1					1			2		3	3	1	1	2	3
Distal end		1									1		1	1	1	1		
Radius																		
Proximal end			1								1			1			2	
Shaft	1	1	1					1			1		1	3			1	1
Distal end			1									1	2	1		1		1
Ulna								1			1		1	1	1		1	
Carpal					1						2	2	1	2	1			1
Metacarpal																		
Proximal end													1	1			3	
Shaft					1						1		2	2				
Distal end											2		1	1				
Pelvis			1							1	1				2		3	1
Femur																		
Proximal end															1		1	1

	Level 1 MNE			Level 2 MNE			Level 3 MNE			Level 4 MNE			Level 5 MNE			Level 6 MNE		
	Small	**Middle**	**Large**	**Small**	**Middle**	**Large**	**Small**	**Middle**	**Large**	**Small**	**Middle**	**Large**	**Small**	**Middle**	**Large**	**Small**	**Middle**	**Large**
Shaft								1			1		1	4		1	1	2
Distal end		1									1	1			1		2	1
Tibia																		
Proximal end											1						1	
Shaft	1	1				1	1	2		2	3		3	5	1	2	6	3
Distal end										1	1		2				1	
Patella																		
Tarsal										1			2	2		1		
Metatarsal																		
Proximal end												1		1	1	1	1	
Shaft								1		2	2		2	2	1	2	3	1
Distal end										1	1		2		1		1	
Metapodial																		
Proximal end		1											1					
Shaft													2				3	
Distal end													1					
Phalange											1	1		2		1	1	
Sesamoid					1					2				1	1			
Total	6	11	25	0	8	6	2	12	3	29	36	24	43	79	32	18	80	25

Level 5 shows a similar pattern. In this level, small-sized animals are well represented by axial and appendicular elements, but cranial bones appear less frequently. Medium-sized species are represented by bones of all sections, but proportionally there is a lack of axial elements and long bone epiphyses. Large-sized animals are as well represented as in Level 4, with a significant scarcity of appendicular elements.

Few elements – mainly appendicular elements – belong to small-sized animals in Level 6. Medium-sized species are mostly represented by appendicular and cranial elements, whereas the axial skeleton appears underrepresented. Finally, large animals show the opposite trend to that seen in Levels 4 and 5, as appendicular elements predominate over axial bones (Table 2).

Each level and each taxonomic group shows a different pattern of representation. Only two global patterns can be detected. First, there is a scarcity of elements in relation to the MNI estimates; this suggests a large preservation bias. Secondly, such bias seems to mainly affect axial elements amongst small- and medium-sized animals. By contrast, the axial skeleton of large species is proportionately better represented than other skeletal sections (Levels 1, 3, 4 and 5). Regarding the proportion of epiphyses vs. shafts, several results can be highlighted (Table 2). In the lower levels, shafts are more abundant than epiphyses, although the differences are not significant; only medium-sized animals in Level 5 show a considerable bias in this regard (Table 2).

The taphonomic study

Taphonomic analyses may help explain the representation bias observed in the assemblage. These indicate that fragmentation was not very intense. In most levels, bones <3 cm make up only 33–50% of the total assemblage. The levels showing a greater fragmentation are Level 4 with 50% of bones <3 cm and Level 2 with 71% of specimens <3 cm (Fig. 4).

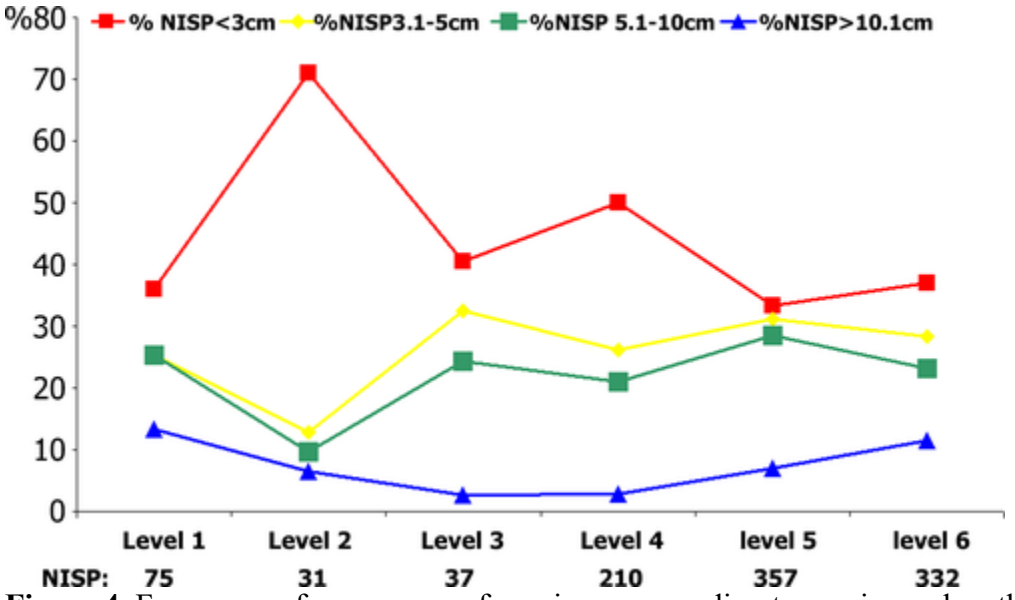

Figure 4. Frequency of occurrence of specimens according to maximum length.

Regarding bone surface modifications, the impact of water is evident. The location of the site in a fluvial palaeochannel resulted in 44.3% (Level 4) and 67.7% (Level 2) of the remains showing hydraulic alterations such as abrasion, polishing and rounding (Table S1). These modifications were identified on the edges of green fractures, which suggests that water acted on previously fractured samples. Water action also resulted in the precipitation of carbonates on the surface of the bones and the appearance of calcareous concretions on a large proportion of the assemblage (Table S1).

The action of water flows could have caused the movement of bones that are more prone to be transported off site. According to Voorhies (1969) and Behrensmeyer (1975, 1982) small and less dense elements are more easily transported by water. This means that epiphyses and axial elements are more likely to disappear than other bones (e.g. mandible).

The representation bias described in Tables 1 and 2 could have been produced by the action of water, as 'transportable' (Voorhies group I) elements such as ribs and vertebrae are scarce. However, this does not explain why other, less easily transported elements such as mandibles are also scarce. This interpretation of water action conflicts with the fact that more than 40% of specimens are <3 cm (Fig. 4). Thus, although water action appears to have affected bone surfaces, it does not explain all of the observed osteological bias.

Other bone surface modifications such as weathering or biochemical alterations are rare (Table S1) and there is a predominance of bones with green fractures (Table S2).

The representation bias may also be explained by the action of carnivores. Some tooth marks were identified on the fossil assemblage, including pits, scores, punctures and furrowing (Tables S3). Notch types C and D, which are usually related to the action of carnivores, were observed in Levels 1 and 3–6 (Table 4).

Tooth mark frequencies are low except in Level 1. Furrowing is not intense (Table 3), and there are usually no more than five tooth marks per bone, even when pits and scores were observed on the same specimen. In addition, epiphyseal representation is not extremely low (Table 2). In Levels 3–6 long bone breakage patterns correspond to type 1 (<50% of the circumference is left) instead of being complete (Fig. 5).

Table 3. Modifications produced by carnivores

Level	**1**	**2**	**3**	**4**	**5**	**6**
NISP with good surface preservation	15	5	22	69	142	129
NISP with tooth marks	5		1	7	11	8
% NISP with tooth marks	33.3		4.5	10.1	7.8	6.2
NISP with furrowing	2 (1 fem., 1 hum.)				1 hum.	1 hum.
% NISP with furrowing respect to long bones	33% hum. and 100% fem.				5.5% hum.	5.5% hum.

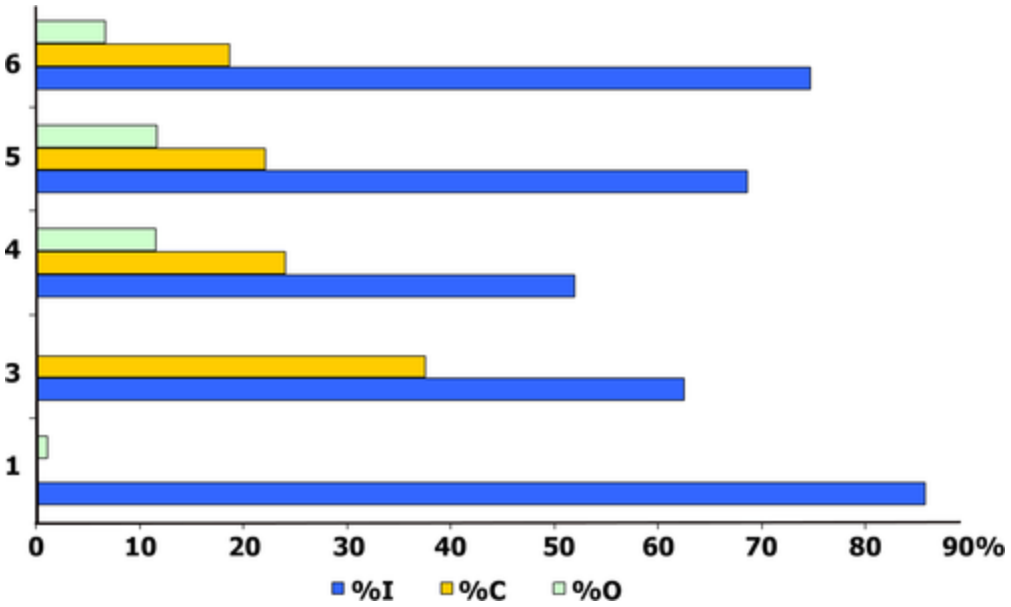

Figure 5. Circumference types for long bones according to Bunn (1982), where I: <50%, C: >50% and O: complete circumference.

Anthropogenic activity was documented in the lower levels of the sequence. Cut marks were identified in Levels 4–6, suggesting defleshing and disarticulation activities (Tables 5, 6). The presence of percussion marks (table 5 and figs S25–S28 of Diez-Martín *et al*. 2015) and the predominance of notch types A and B in Levels 3–6 (Table 4) suggest that in addition to defleshing activities, hominins also extracted the marrow from some long bones. There are several percussion marks on the long bone shafts (tibiae, radii, humeri) of medium-sized individuals (4–5). The recovery of three impact flakes belonging to size 3/3b animals in Levels 5 and 6 also points to an anthropogenic contribution to the assemblage.

Table 4. Frequency of notch types at FLKW according to the types defined by Capaldo & Blumenschine (1994) and Domínguez-Rodrigo *et al*. (2007)

Level	**1**	**2**	**3**	**4**	**5**	**6**
Notches	1		1	2	7	7
Notches Type Single (a)			1 (100)	1 (50)	3 (43)	3 (43)
Notches Type Incomplete (b)					2 (29)	1 (14.3)
Notche Type Double (c)	1 (100)			1 (50)	1 (14)	3 (43)
Notches Type Opposing (d)					1 (14)	

Table 5. Main human modifications at FLKW

Level	**1**	**2**	**3**	**4**	**5**	**6**
NISP with good surface preservation	15	5	22	69	142	129
NISP with cut marks				1	4	1
% NISP with cut marks				1.5	2.8	0.8
NISP with percussion marks			3	1	8	9
% NISP with percussion marks			13.6	1.5	5.6	7

Table 6. Anatomical distribution of cut marks at FLKW

Anatomical distribution	Animal size	Level 4	Level 5	Level 6
Femur shaft	3	Defleshing		
Metatarsal shaft	4		Defleshing	
Rib	3		Disarticulation	
Tibia shaft	4		Defleshing	
Humerus shaft	3a		Defleshing	
Tibia shaft	3b			Defleshing or disarticulation

The notch angles are either very acute (66°) or very obtuse (120°), which matches the pattern produced by human activity. It is still unknown whether humans were primarily responsible for the accumulation of carcasses at FLKW. However, it seems clear that hominins had access to meat resources, as evidenced by the cut marks on diaphyseal sections of upper limb bones (e.g. humerus and femur; Table 6). It has also been demonstrated that hominins practiced an intensive exploitation of the resources to obtain the marrow.

Geometric morphometric and micro-photogrammetric analysis of cut marks

As we detected a clear association between the fauna and lithic industry at FLKW, we decided to conduct an analysis to determine the kind of tools used at FLKW for the exploitation of the carcasses. The presence of handaxes in the same space as bones with cut marks could suggest that handaxes were used to process the carcasses. Here we present the results obtained after a detailed analysis of FLKW cut marks that involves the creation of 3D models. Such models are based on the use of oblique photography with a reflex camera with a macro-lens (average GSD (mm) = ±0.0078; average scaling error (mm) = ±0.0157; average photogrammetric error (mm) = ±0.0058; average precision (mm) = ±0.0168).

Our high-quality 3D reconstructions show cut marks with a U-shaped section (Figs 6-8). This shape has been traditionally used to define scores generated by teeth, instead of cut marks that are usually described as V-shaped marks (Binford 1981). Thus these results could generate some confusion. However, it must be taken into account that the FLKW marks were affected by the action of water. All the bones with cut marks show a certain degree of polishing and abrasion, which has generated cut marks with U-shaped (Figs 6, 8) or open V-shaped (Figs 7, 8) cross-sections.

Keeping this in mind, we compared the FLKW cut marks with those created in previous experiments with flakes and handaxes made from quartzite and flakes made from basalt. PCA results including biometric data (Figs 9, 10) show that the FLKW cut marks are different from those generated in our experiments using a quartzite handaxe (Fig. 9A, B). The marks generated with the experimental quartzite handaxe are also different from those created with quartzite and basalt flakes (Fig. 9). Cut marks produced with the experimental handaxe are wider as a result of the double-sided tool edge. The FLKW marks fit with the group that includes the marks produced with quartzite flakes (Fig. 9A, B), being slightly different from those produced with basalt flakes (Fig. 9A). These results suggest that the FLKW marks were generated with simple (probably quartzite) flakes rather than handaxes.

Figure 6. Cut mark on a metatarsal and its cross-section. The cross-section was obtained with the aid of photogrammetric means.

Figure 7. Cut marks on a femur and their cross-sections. The cross-sections were obtained with the aid of photogrammetric means.

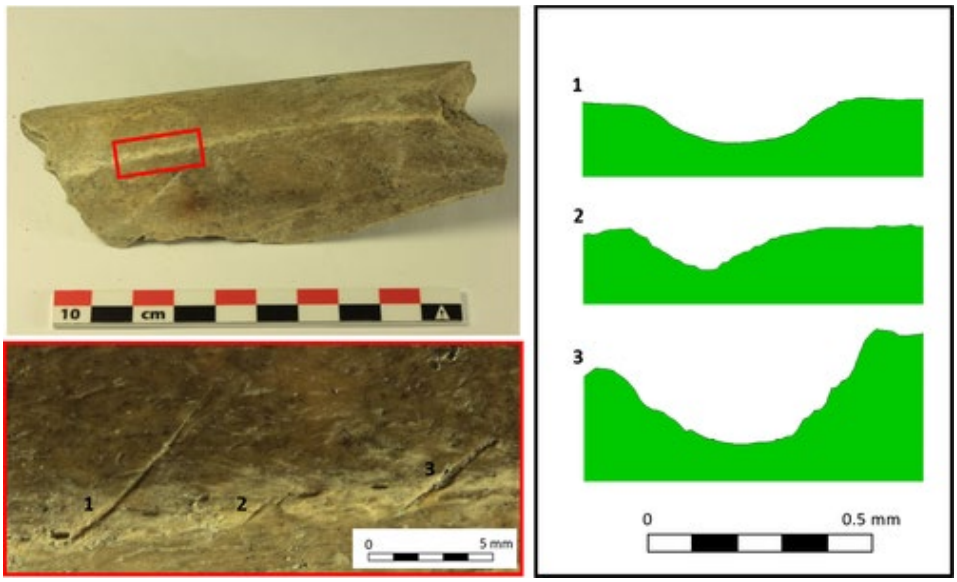

Figure 8. Cut marks on a tibia and their cross-sections. The cross-sections were obtained with the aid of photogrammetric means.

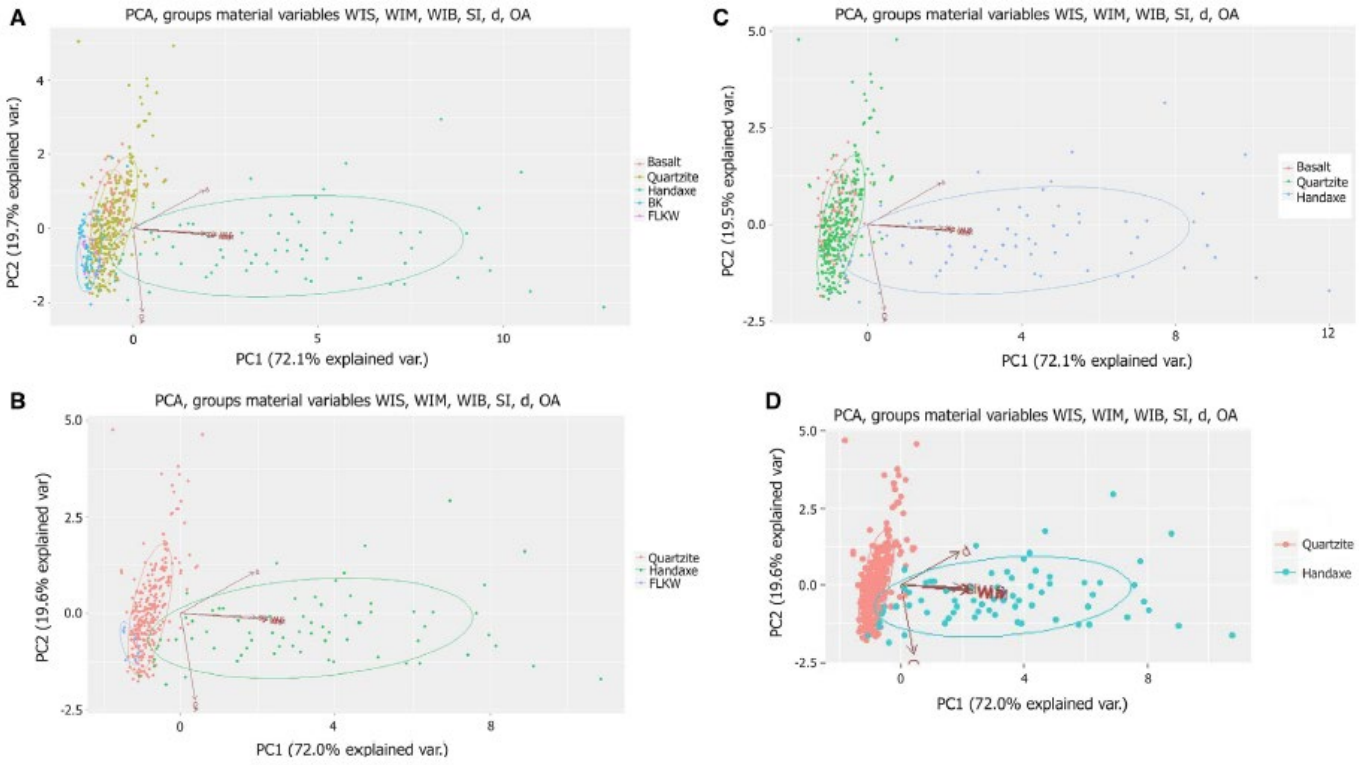

Figure 9. PCA plot comparing cut marks produced with: A. Simple quartzite and basalt flakes with those generated with the experimental quartzite handaxe, and the cut marks identified at BK and FLKW. B. Simple quartzite flakes with those generated with the experimental quartzite handaxe, and the cut marks identified at FLKW. C. Simple quartzite and basalt flakes with those generated with the experimental quartzite handaxe. D. Simple quartzite flakes with those generated with the experimental quartzite handaxe. See 4 section for detailed description of WIS, WIM, WIB, SI, d, OA.

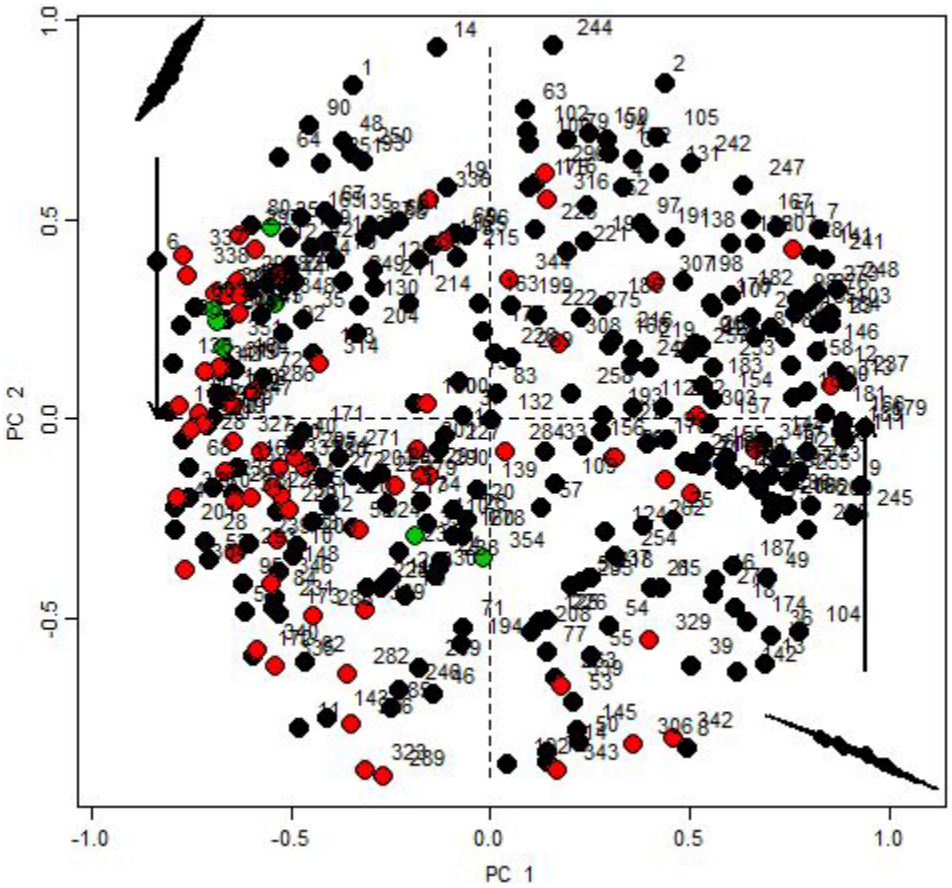

Figure 10. PCA plot of the morphometric analysis, where cut marks identified at FLKW are plotted in green, cut marks produced with simple quartzite flakes are red and cut marks generated with the experimental quartzite handaxes are black.

It should be noted that the experimental handaxe marks are not only different from those produced with simple quartzite and basalt flakes but also from the cut marks identified at Bed II sites such as BK (Fig. 9A, C). The PCA results including morphometric data (Fig. 10) show the same results as in Fig. 9. The FLKW marks cluster with cut marks produced with simple flakes.

Following the experimental work with handaxes of Bello *et al*. (2009) in Boxgrove and their conclusions, it should be stressed that morphological differences amongst cut marks can be the result of different levels of hand pressure rather than the use of different types of raw materials or tool. However, as the FLKW cut marks were clustered with the cut marks made with quartzite flakes and the BK cut marks (Fig. 9A, B), we opted for this interpretation, given the lack of proper experimental analogues for documenting how hand pressure impacts the morphological range of cut marks.

Although the cut marks at FLKW were not produced with handaxes, the presence of percussion marks and bones with green fractures on the site could allow the interpretation that bones were broken using handaxes. However, this can only be considered as a possibility. Choppers and hammers are frequent in FLKW and those could also have been used to break the bones. Only

future experimental bone-breaking analyses with handaxes will allow us to know if handaxes were used in the breakage of bones at the site.

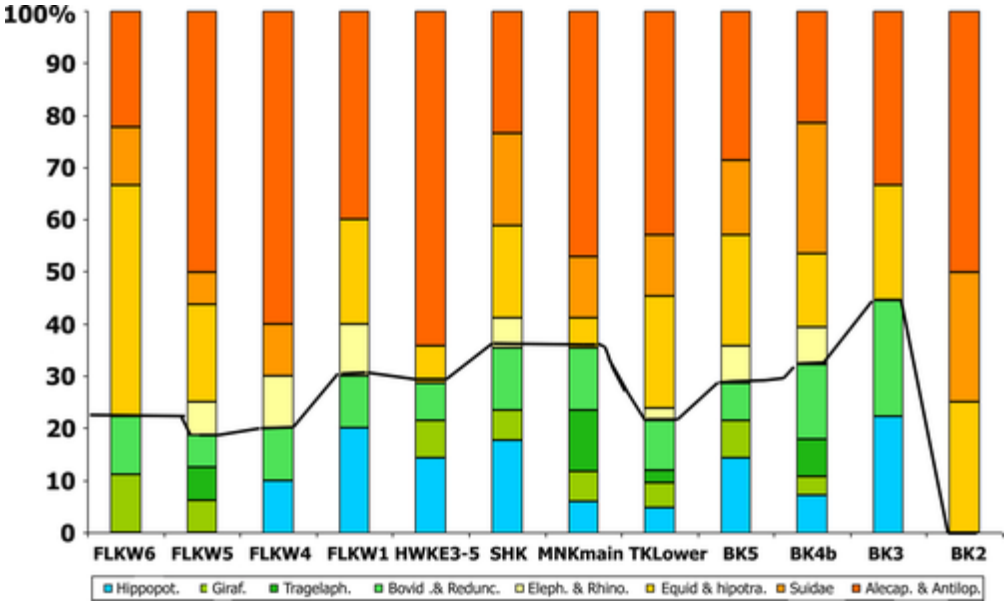

Figure 11. Faunal representation and MNI at the main Bed II sites.

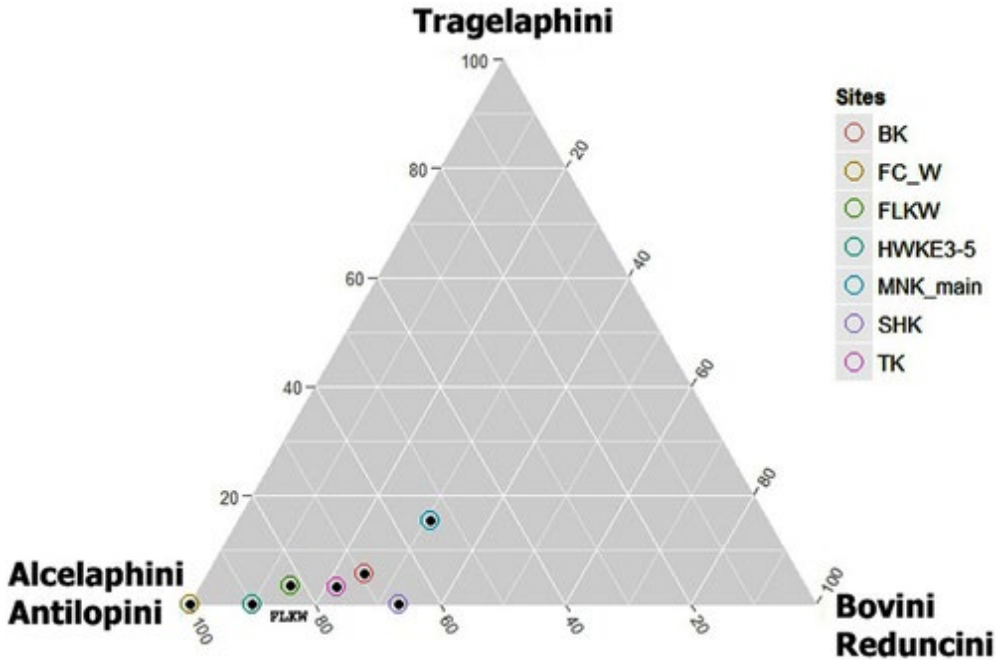

Figure 12. Ternary graph programmed in R, using all the data from each bovid group (Alcelaphini and Antilopini, Reduncini and Bovini, and Tragelaphini and Aepycerotini) found at different Olduvai sites.

Palaeoecological analyses

Palaeoecological analyses indicate that the landscape surrounding FLKW was open (Figs 11, 12). Animals adapted to open areas such as Alcelaphini, equids, Suidae, Antilopini, Rhinocerontidae and Proboscidea appear in the studied FLKW levels. Species more suited to forested habitats and hippopotamus are scarce and do not exceed 30% of the MNI. These patterns are consistent with the trends observed at other Bed II sites. For example, at HWKE, open-habitat species also make up 70% of the total MNI (Fig. 11).

The bovid record of several Olduvai Bed II sites (e.g. SHK, TK, BK) shows a predominance of species adapted to open environments (Fig. 12), which confirms previous interpretations on the openness of landscapes during Bed II times (Domínguez-Rodrigo *et al*. 2014a, b).

Conclusions

Several conclusions can be drawn from this study. On the one hand, the taphonomic analysis demonstrated that the FLKW fossil assemblage was not created by abiotic external processes (e.g. the action of water), although it was impacted by them. The presence of a large amount of small bone fragments, and a significant number of epiphyseal and axial elements indicate that water flows did not play a major role in the formation of the site. On the other hand, the identification of certain surface modifications associated with the action of water such as polishing, rounding and abrasion indicate the presence of at least low-to-moderate energy water flows that transported abrasive sediments that ultimately altered the bone surfaces and may even have created assemblages.

Skeletal profiles show that many anatomical elements are missing. Even though only a small area of the site has been excavated, we found some evidence that might explain the bias identified at FLKW. The activity of carnivores was documented in the form of tooth marks and notches. Although carnivore impact is not very significant, especially in Levels 4–6, it could have affected the original representation of the fossil record at FLKW.

Regarding human activity, FLKW appears to be one of the first early Acheulean sites showing a clear functional association between some of the fauna and the lithic assemblage. There are some other Acheulean sites (e.g. TK) where carcasses appear in association with stone tools, but no cut marks could be identified to demonstrate their functional association. At FLKW, cut and percussion marks as well as notch type distribution suggest that some large animals (sizes 3–5) were processed by humans.

The impact of humans on the FLKW assemblage, especially in Levels 4–6 is worth discussing. Even though data are scarce, we have enough evidence to hypothesize about the degree of anthropogenic impact on the site. Although cut marks do not appear in abundance, their anatomical location on the midshafts of long bones (e.g. femur and humerus) and on ribs suggest early access to meat. Levels 4–6, which preserve more significant human activity in the form of cut and percussion marks than the other levels, show a lesser degree of carnivore action. In these levels tooth mark frequencies are low and epiphyses are relatively common. Future excavations and the analysis of new recovered material will provide more complete results. Currently available data suggest that humans played a role in the modification of the FLKW fossil collection, but no definite conclusions can be drawn at this point.

The photogrammetric and morphometric analyses of cut marks suggest that the marks were produced with quartzite flakes instead of handaxes. Thus, the FLKW handaxes do not seem to be related to the exploitation of carcasses, which suggests that these tools were used for different purposes.

Finally it should be noted that FLKW demonstrates the existence of open landscapes during lower Bed II times at Olduvai. Open habitats have already been observed in the upper levels of Bed I at sites like FLKN and probably spread during Bed II times.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at http://www.boreas.dk.

Fig. S1. Handaxe used in the experimentation.

Table S1. Principal chemical and physical alterations affecting the FLKW fossil assemblage.

Table S2. Dry and green breakage patterns on the FLKW long bones.

Table S3. Distribution and description of FLKW tooth marks.

Data S1. Methods of 3D modelling of cut mark sections